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☐	L1	apomixis or apomictic	189
☐	L2	facultative or facultatively	2629
☐	L3	hybridizing	37202
☐	L4	ovule adj development	44
☐	L5	(doubling near5 chromosome) and (spindle adj inhibitor)	7
☐	L6	(doubling near5 chromosome) and colchicine	369
☐	L7	(doubling near5 chromosome) and (B near3 hybridization)	20
☐	L8	allopolyploid or (segmental adj allopolyploid)	20
☐	L9	autopolyploid	11
☐	L10	john near5 carman.in.	20
☐	L11	800/260,266,269,270,271,276,298.ccls.	2990
☐	L12	L1 and L2	12
☐	L13	L12 and L3	7
☐	L14	L13 and L4	4
☐	L15	L14 and L5	3
☐	L16	L14 and L6	3
☐	L17	L14 and L7	2
☐	L18	L16 and (L8 or L9)	3
☐	L19	L1 and L10	4
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=> s apomixis or apomictic
L1      4747 APOMIXIS OR APOMICTIC

=> s facultative or facultatively
L2    315121 FACULTATIVE OR FACULTATIVELY

=> s hybridizing
L3      5580 HYBRIDIZING

=> s ovule(w)development
L4       750 OVULE(W) DEVELOPMENT

=> s (doubling(5a)chromosome) and (spindle(w)inhibitor)
L5         0 (DOUBLING(5A) CHROMOSOME) AND (SPINDLE(W) INHIBITOR)

=> s (doubling(5a)chromosome) and colchicine
L6       624 (DOUBLING(5A) CHROMOSOME) AND COLCHICINE

=> s (doubling(5a)chromosome) and (B(5a)hybridization)
L7         6 (DOUBLING(5A) CHROMOSOME) AND (B(5A) HYBRIDIZATION)

=> s allopolyploid or (segmental(w)allopolyploid)
L8      1007 ALLOPOLYPLOID OR (SEGMENTAL(W) ALLOPOLYPLOID)

=> s autopolyploid
L9       328 AUTOPOLYPLOID

=> s carman j/au
L10       52 CARMAN J/AU

=> s L1 and L2
L11      577 L1 AND L2

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=> s L11 and L4
L13        4 L11 AND L4

=> s L11 and L6
L14        3 L11 AND L6

=> s L11 and L7
L15        0 L11 AND L7

=> s L11 and (L8 or L9)
L16        7 L11 AND (L8 OR L9)

=> s L1 and L10
L17        0 L1 AND L10

=> s L11 and L10
L18        0 L11 AND L10
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L13 ANSWER 1 OF 4 CABA COPYRIGHT 2005 CABI on STN
TI Activity and localisation of sucrose synthase and invertase in ovules of
    sexual and ***apomictic*** Brachiaria decumbens.
SO Protoplasma, (1999) Vol. 208, No. 1/4, pp. 173-185. 36 ref. Price:
    Conference paper; Journal article . Meeting Info.: Proceedings of the 15th
    International Congress on Sexual Plant Reproduction, Wageningen,

AU   Dusi, D. M. A.; Willemse, M. T. M.

L13 ANSWER 2 OF 4 BIOSIS COPYRIGHT (c) 2005 The Thomson Corporation on S
TI   The genetic and molecular analysis of   ***apomixis***   in the model
plant Hieracium.
SO   Acta Biologica Cracoviensia Series Botanica, (2000) Vol. 42, No. 2, pp.
61-72. print.
CODEN: ABCBAM. ISSN: 0001-5296.
AU   Koltunow, Anna M. [Reprint author]

L13 ANSWER 4 OF 4 BIOSIS COPYRIGHT (c) 2005 The Thomson Corporation on S
TI   STUDIES IN CRATAEGUS ROSACEAE MALOIDEAE XIX. BREEDING BEHAVIOI
CANADA CRATAEGUS SERIES ROTUNDIFOLIAE.
SO   Canadian Journal of Botany, (1988) Vol. 66, No. 10, pp. 1914-1923.
CODEN: CJBOAW. ISSN: 0008-4026.
AU   SMITH P G [Reprint author]; PHIPPS J B

L14 ANSWER 1 OF 3 CABA COPYRIGHT 2005 CABI on STN
TI   A rise of ploidy level induces the expression of   ***apomixis***   in
Paspalum notatum.
SO   Sexual Plant Reproduction, (2001) Vol. 13, No. 5, pp. 243-249. 24 ref.
Publisher: Springer-Verlag.
ISSN: 0934-0882
AU   Quarin, C. L.; Espinoza, F.; Martinez, E. J.; Pessino, S. C.; Bovo, O. A.

L14 ANSWER 2 OF 3 CABA COPYRIGHT 2005 CABI on STN
TI   [The breeding of   ***apomictic***   varieties of Panicum maximum].
L'amelioration genetique des varietes apomictiques de Panicum maximum.
SO   Garcia de Orta, Estudos Agronomicos, (1983) Vol. 10, No. 1/2, pp. 161-168.
8 ref.
AU   Noirot, M.

L16 ANSWER 1 OF 7 CABA COPYRIGHT 2005 CABI on STN
TI   Comparative analysis of genetic divergence among sexual ancestors of
apomictic   complexes using isozyme data.
SO   International Journal of Plant Sciences, (2004) Vol. 165, No. 4, pp.
615-622. 48 ref. Publisher: University of Chicago Press.
ISSN: 1058-5893
URL: http://www.journals.uchicago.edu/IJPS/journal/
AU   Horandl, E.

L16 ANSWER 2 OF 7 CABA COPYRIGHT 2005 CABI on STN
TI   Reproduction mode in the   ***allopolyploid***   ***facultatively***
apomictic   hawkweed Hieracium rubrum (Asteraceae, Hieracium subgen.
Pilosella).
SO   Hereditas (Lund), (2004) Vol. 141, No. 1, pp. 19-30. 42 ref. Publisher:
Mendelian Society.
ISSN: 0018-0661
AU   Krahulcova, A.; Papouskova, S.; Krahulec, F.

L16 ANSWER 6 OF 7 BIOSIS COPYRIGHT (c) 2005 The Thomson Corporation on S
TI   ***Apomixis***   and hybridity in Hypericum perforatum.
SO   Folia Geobotanica et Phytotaxonomica, (1996) Vol. 31, No. 3, pp. 389-396.
CODEN: FGPHAP. ISSN: 0015-5551.
AU   Martonfi, Pavol; Brutovska, Renata; Cellarova, Eva; Repcak, Miroslav

L16 ANSWER 7 OF 7 BIOSIS COPYRIGHT (c) 2005 The Thomson Corporation on S
TI   Evolutionary significance of   ***apomixis***   in the genus Sorbus
(Rosaceae).
SO   Fragmenta Floristica et Geobotanica, (1993) Vol. 38, No. 2, pp. 627-686.
CODEN: FRFGAF. ISSN: 0015-931X.
AU   Jankun, Andrzej

3

Apomixis and its Application in Crop Improvement

E. C. Bashaw

USDA-SEA and Texas A&M University
College Station

Seed is formed in some species of higher plants by an asexual method of reproduction called apomixis. The apomictic seed develops in the ovary, as in sexually reproducing plants, but the embryo is formed without union of the sperm and egg. As a rule, the embryo originates by mitotic division of a nucleus in a somatic cell of the ovule and the male gamete does not fuse with the nucleus. Except in special types of apomixis, the zygote has exactly the same chromosome complement and genetic constitution as the mother plant and the offspring is a true clone, just as if it had developed from a vegetative organ. Hybridization between completely apomictic plants, also called obligate apomicts, is impossible except in rare instances when the sperm may unite with the unreduced nucleus of the female. Unless a mutation occurs in an obligate apomict, there is no natural variation among the progeny from which to select new types. Were it not for the fact that sexual or partially sexual plants can be found in most apomictic species, there would be little prospect for improvement through breeding.

For many years, apomixis was considered a total barrier to plant breeding and most geneticists were not anxious to find apomixis in the species they sought to improve. Darlington (1939) expressed the thinking of scientists of his time in a statement that, "apomixis is an escape from sterility, but an escape into a blind alley of evolution," inferring that all apomicts are doomed for extinction. As basic research on reproductive systems and breeding problems increased, it became apparent that apomixis is not a rare phenomenon in the plant kingdom and certainly is not an evolutionary "blind alley." Plant scientists have encountered apomixis again and again in diverse, unrelated, plant families, indicating that it is widespread, but often unnoticed in many genera. Some form of apomixis has been reported

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in at least 30 families of higher plants, including more than 300 species (Gustafsson, 1947; Nygren, 1954, 1967).

We now recognize that apomixis is the most common method of reproduction in many species of *Citrus* and berries, as well as guayule and numerous perennial forage grasses. Apomixis recently has been reported in grain sorghum and pearl millet and is believed to be present in several other important crops. Breeders of certain forage grasses have long been challenged to overcome the problems of reproductive isolation created by apomixis. Plant scientists have devoted considerable effort to investigations of the cytological and genetic basis of apomixis. These studies and the discovery of sexual plants in species previously thought to be completely apomictic eventually led to a new concept of apomixis in plant improvement—the possibility of controlling and manipulating apomixis as a plant breeding tool. Complete control of apomixis would afford the breeder and producer a system having the efficiency of reproduction through vegetative organs, but with the convenience of propagation through asexually developed seed. The most significant achievement, however, would be the ability to combine the desirable characteristics of two parents and simultaneously produce true-breeding apomictic F_1 hybrids with permanently fixed heterosis. Successful breeding programs recently have been developed with a few apomictic forage grasses by crossing a sexual plant with obligate apomicts and selecting and testing their apomictic F_1 hybrids.

To determine the potential for breeding an apomictic species, it is necessary to understand the apomictic mechanisms involved and to know if sexual reproduction occurs in the species. Individual plants of some species (Kentucky bluegrass, sorghum, guayule), called facultative apomicts, are capable of both sexual and apomictic reproduction in the same ovule. Some offspring from these plants are identical to the mother plant (apomictic origin) while others are different and variable (sexual origin). Since it is impossible to control method of reproduction in the ovules of facultative apomicts, the breeding of these species poses special problems because of unpredictable progeny variation (Section VI B).

I. MECHANISMS OF APOMIXIS

The mechanism of apomixis refers to the cytological basis for embryo development which determines the genetic constitution of the offspring. Many authors favor a broad definition of apomixis that includes reproduction through purely vegetative organs such as rhizomes, stolons, and buds; however, plant breeders tend to restrict the term to asexual seed formation. This chapter concerns only the gametophytic generation. Apomixis will be used in this chapter to designate only those mechanisms for asexual seed development, collectively called agamospermy. There are four major mechanisms for agamospermy: apospory, diplospory, adventitious embryony, and parthenogenesis. The distinction among mechanisms is based on the site of origin and subsequent developmental pattern of the cell which gives rise to the embryo. Origin and development can be determined by cytological studies of young ovaries at the stage when megasporogenesis and embryo sac development would be expected to occur.

In the following discussion, photomicrographs will be used to compare sexual and apomictic development in ovules at critical stages required for identification of apomictic mechanisms. Megasporogenesis and development of the embryo sac in a typical sexual ovule are shown in Figs. 1A to F. The megaspore mother cell differentiates from a cell in the second (hypodermal) cell layer of the nucellus near the micropyle before the integuments are fully developed (Fig. 1A). At this stage, the orientation of the micropyle of the young ovule is at a right angle to the vertical axis of the ovary. Meiosis results in a linear tetrad of megaspores and soon after the second meiotic division the three megaspores nearest the micropyle disintegrate (Fig. 1B). The nucleus of the remaining megaspore divides and the two daughter nuclei migrate to opposite ends of the cell (Fig. 1C). Each nucleus undergoes two additional divisions producing an eight-nucleate embryo sac, which differentiates to form a mature gametophyte with two synergids, an egg, two polar nuclei, and three antipodals (Fig. 1D). Often the synergids disintegrate very early and in some species, especially of the Gramineae, the antipodals may continue to divide and form a cluster of cells (Fig. 1E) at the tip or side of the embryo sac. In many sexual species, remnants of the antipodals persist after embryo and endosperm begin to develop (Fig. 1F).

A. Apospory

In apospory, the embryo and endosperm develop in unreduced embryo sacs derived from somatic cells at various locations in the ovule. A normal megaspore mother cell develops in the same manner described for the sexual ovule and begins to undergo meiosis, but in apospory it may or may not complete both divisions to form a linear tetrad of megaspores. During this stage one or more somatic cells in the ovule and their nuclei begin to enlarge and usually resemble megaspore mother cells (Fig. 2A). The meristematic appearance of these cells contrasts sharply with that of the surrounding somatic cells, which remain inactive or senescent. At some stage, usually before a mature sexual embryo sac is formed, the megaspore or young sexual embryo sac aborts and is replaced by the developing aposporous sacs. The appearance of an ovule with developing aposporous cells (Figs. 2B and C) is quite different from that of a sexual ovule which will have a single sexual sac. For example, compare Fig. 2B and C with the two-nucleate sexual sac in Fig. 1C. In grain sorghum and some other species, initiation and development of aposporous embryo sacs may occur much later.

The nuclei in some aposporous cells undergo one or more mitotic divisions and the cells may enlarge considerably, but nuclear division and cell enlargement vary even in the same ovule. At the mature embryo sac stage, the ovule contains one or more enlarged aposporous cells with varying numbers of unreduced nuclei (Figs. 2D and E). These cells tend to resemble embryo sacs, but differentiation within the sacs is variable. Differentiation is always very limited in some species (buffelgrass and dallisgrass), and their aposporous sacs never contain the antipodals present in sexual embryo sacs. In these species, apospory is easy to distinguish from sexual development in mature ovules by the absence of antipodals and lack of organization within the aposporous sac. The contrast between undifferentiated aposporous sacs and sexual embryo sacs may be observed by comparing Figs. 2D and E with

Figs. 1D and E. However, in some species (Kentucky bluegrass and grain sorghum) one or more of the aposporous sacs may differentiate fully and look exactly like a sexual embryo sac at anthesis. In these species, it is necessary to follow the early development of embryo sacs to accurately identify apospory and to determine if the sexual embryo sac also develops.

Apospory is by far the most common mechanism of apomixis in higher plants. In most species it is characterized by the presence of multiple "embryo sacs," however, some aposporous species characteristically form a single embryo sac, which may or may not resemble a sexual sac.

B. Diplospory

In diplospory, the embryo and endosperm develop in an unreduced embryo sac derived from the megaspore mother cell. The megaspore mother cell (Fig. 2F) differentiates like that of sexual ovules, but its nucleus does
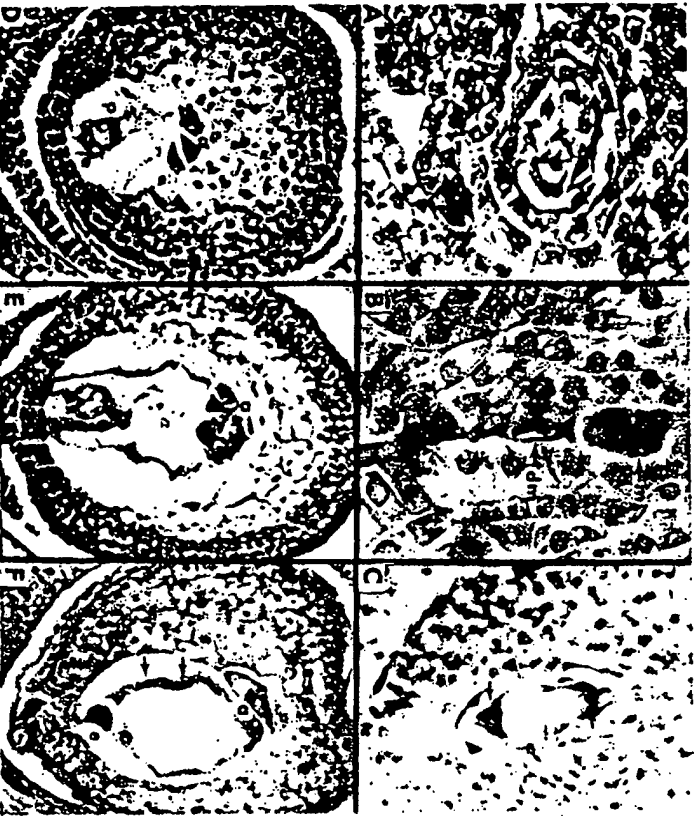

Fig. 1—Origin and development of embryo sacs in ovules of a sexual forage grass. A. Differentiated megaspore mother cell. B. Functional megaspore (m) and remnants of three degenerated megaspore (dm). C. Early embryo sac with two nuclei (arrows). D. Mature sexual embryo sac with egg (e), polar nuclei (p), and antipodals (a). E. Sexual embryo sac with antipodal cluster (a). Synergids have disintegrated at mature embryo sac stage. F. Early embryo (arrows) and endosperm (arrows) with remnants of antipodals (a).
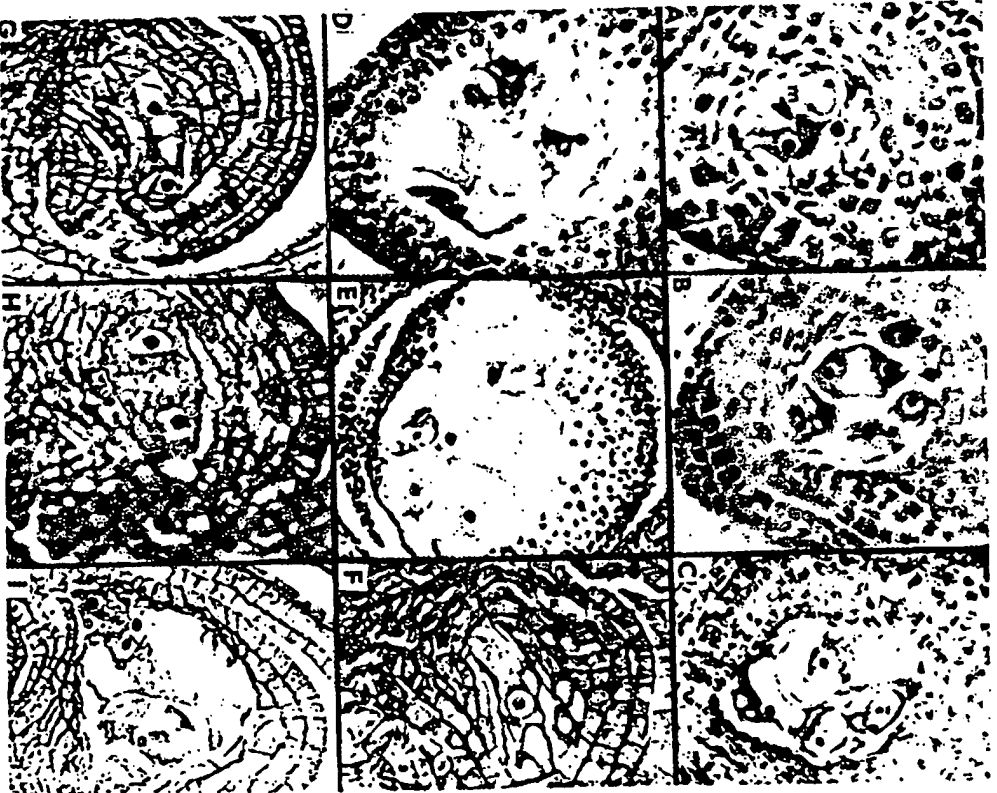
Fig. 2—Origin and development of embryo sacs in ovules of aposporous and diplosporous forage grasses. Apospory: A. Aposporous cells (arrow) developing adjacent to degenerated megaspore (m), B to D. Aposporous cells in various stages of development (note resemblance to sexual egg and polar nuclei in Fig. 1D arrow). E. Multiple aposporous embryo sacs in mature ovule (note absence of antipodal cells). Diplospory: F. Megaspore mother cell. G. Unreduced embryo sac with two nuclei. H. Two-nucleate embryo sac and remnants of degenerated megaspores (arrow) in a sexual ovule. I. Fully differentiated diplosporous embryo sac with egg (e), polar nuclei (p), and antipodals (a).

not undergo meiosis. Instead, the nucleus divides mitotically and the cell enlarges considerably, but does not divide. Eventually this cell fills the area that the linear tetrad would occupy in sexual ovules. After the first division of the nucleus, the nuclei migrate to opposite ends of the cell (Fig. 2G) and may closely resemble the two-nucleate stage of a sexual embryo sac (Fig. 2H). However, the two-nucleate sexual sac usually develops nearer the center of the ovule and remnants of degenerated megaspores may be visible toward the micropyle. Further division of the nuclei and differentiation of diplosporous embryo sacs varies with different species.

In the few known diplosporous species of agronomic crops, the embryo sac differentiates normally and, when mature, it looks exactly like the sexual embryo sac of the species (Fig. 2I). Cytological identification of diplospory is usually impossible at or beyond the two-nucleate embryo sac stage. The area of the ovule, other than the megaspores and embryo sac, is completely normal and shows no evidence of apomixis. The cytologist must carefully follow the early developmental stages to be certain of the origin of the embryo sac. The absence of meiosis and a linear tetrad of megaspores is the best evidence of diplospory.

There are other forms of diplospory in which meiosis is initiated, but the embryo sac receives the unreduced chromosome number either due to failure of reduction division or spontaneous doubling of the chromosome number of the functional megaspore after meiosis. When chromosome doubling occurs after meiosis, the progeny of heterozygous plants will not be uniform. This type of diplospory has not been reported in species of agronomic importance and is of little concern to plant breeders at this time.

C. Adventitious Embryony

In adventitious embryony, the embryo develops in somatic cells of the ovule, integuments, or ovary wall and is initiated as a bud-like structure through mitotic division of the cell nucleus. No embryo sac is formed, and in the early stages of development these embryonic structures resemble bud tissue or the globe stage of a developing proembryo. Eventually this mass of rapidly dividing cells differentiates and forms a typical embryo. No polar nuclei are associated with these embryos because there is no embryo sac. Little is known about the later stages of development, but it is assumed that in species in which endosperm develops, it must arise from polar nuclei in normal embryo sacs.

Adventitious embryony is the usual mechanism of apomixis in Citrus species. It is rare in other higher plants, but this mechanism has been observed occasionally in some grasses, usually along with apospory.

D. Parthenogenesis

A parthenogenic embryo develops directly from the reduced egg nucleus in a sexual embryo sac without fertilization by the sperm (haploidy). This phenomenon probably occurs occasionally in all sexual species, and it cannot be identified cytologically. Parthenogenesis is usually

detected by the presence of haploid offspring. Normally parthenogenesis is infrequent, random, and spontaneous. However, the tendency for parthenogenesis in lines of some species (corn, cotton) is genetically controlled.

Use of the term parthenogenesis in plant literature is often confusing and varied. Some define it as development of an embryo from any presumed "egg cell" without pollination, regardless of the origin of the embryo sac. In aposporous apomicts, there is often no basis for designating a particular nucleus as the egg. Initiation of embryonic development without pollination occurs frequently in some species and the role of pollination is problematical. For the plant breeder, restriction of the term parthenogenesis to the familiar phenomenon of haploidy appears to be a logical solution to the confusion encountered in the literature.

E. Special Cases

There are some unusual reproductive phenomena that might properly be classified as apomixis. Androgenesis refers to a rather rare form of haploidy in which the embryo develops directly from the sperm after it enters the embryo sac. Apparently this is a non-recurrent event in most species and poses little or no problem or opportunity for plant breeding. However, genetic control of androgenesis has been reported in some lines of corn (Kermicle, 1969).

A rare form of parthenogenesis, called semigamy, has been reported in some species, including Pima cotton (Turcotte and Feaster, 1969). A sperm nucleus penetrates the egg cell but does not fuse with the egg nucleus. Subsequently, the egg and sperm nuclei divide independently, a process resulting in a heterogeneous haploid embryo that contains sectors of both male and female origin. Turcotte and Feaster (1969) were able to produce homozygous lines of Pima cotton by using colchicine to double the chromosomes in cells of the different sectors in haploid plants derived from the haploid embryos. Results of breeding studies showed that semigamy was controlled genetically in some lines.

Sometimes an unreduced egg nucleus in an apomictic embryo sac is fertilized by the sperm. There is no information available on the frequency of fertilization of an unreduced egg, but it has been reported in numerous species. While this is not a true form of apomixis, according to the classical definition of the term, its occurrence has considerable significance. For example, this represents one important method for natural increase in ploidy level in apomictic species because a whole genome from the male parent is added to the chromosome complement of the mother plant. Implications of this process in the breeding of apomicts are discussed in Section VI.

II. EMBRYO DEVELOPMENT IN APOMICTS

Although the embryo is formed without union of the male and female gametes, pollination is necessary in many apomicts for full development of the embryo and endosperm. The term pseudogamy denotes that pollination

is an absolute requirement for development of a viable seed. The role of pollination in apomicts is not fully understood, but it is assumed to function as a stimulus for initiation of embryo and endosperm development, for fertilization of the polar nuclei, or as a requirement for full maturation of the embryo.

The apomictic grasses are generally pseudogamous and, in most species, it seems that the polar nuclei must be fertilized before the endosperm can develop. Chromosome counts of dividing endosperm cells have confirmed fertilization of the polar nucleus or nuclei in a few species. However, it is impossible to obtain clear and conclusive results in most cases because of the dense cytoplasm present in endosperm cells. Initiation of embryo development before pollination has been observed in ovules of apomictic species of *Poa*, *Paspalum*, *Cenchrus*, and many other grass genera, but the endosperm did not develop and the embryo did not differentiate until after pollination. In most ovules, neither the embryo or endosperm develops until after pollination.

Development of the embryo and endosperm of apomicts after pollination usually follows the normal pattern of sexual plants in the species. There is no apparent difference in the embryology of sexual and apomictic plants of *Cenchrus*, *Paspalum*, and *Poa*, except when the embryo starts to develop before pollination. In these cases, cell division of the embryo usually stops before or at the globe stage and there is no further development until pollination. After pollination, the endosperm cells usually divide several times before any perceptible change is seen in the proembryo. In the absence of embryo development before pollination, first division of the unreduced egg nucleus usually occurs after the endosperm starts to develop. Subsequent growth and differentiation is generally not different from normal development described in Chapter 2.

In aposporous apomicts, development of two or more embryos is quite common. Usually one embryo will be situated in the normal position and others may appear at random in the ovule. Initially, endosperm may develop in more than one aposporous embryo sac, but apparently these fuse during development and form a uniform endosperm in the mature seed.

III. INDICATORS OF APOMIXIS

There is nothing about the appearance of a single apomictic plant that suggests apomixis, but its progeny will have certain characteristics that may serve as useful indicators of apomictic reproduction. Detection of apomixis on the basis of morphological indicators requires careful observation of the progenies of individual plants by a person who is thoroughly familiar with mode of pollination of the parent and the variability expected among its sexually produced offspring. For example, lack of variation among the progeny of a heterozygous or cross-pollinated plant and production of offspring that closely resemble the maternal parent suggest apomixis. These same characteristics are expected in the progenies of homozygous, self-pollinated, sexual plants and would not cause one to suspect apomixis in them.

Obligate apomixis can usually be recognized easily in a heterozygous or cross-pollinated species. The offspring of obligate apomicts are completely uniform and all are identical to the maternal parent. The striking uniformity of an obligate apomict will usually be apparent when new accessions are first evaluated, unless the seed has been mixed. A progeny test of variant plants should be conducted using open-pollinated seed to determine if these plants are sexual, partially sexual (facultative), or simply plants of a different apomictic strain. It is unlikely that obligate apomictic plants will appear suddenly in a plant breeding program of sexual species. If, however, the progeny of a hybrid or selection fails to segregate as expected, it should be suspected as a possible apomict and subjected to further evaluation. Such a plant could be a valuable asset to the breeder for reasons discussed in Section VI.

Detecting facultative apomixis may be considerably more difficult, but the same indicators and principles apply. Facultative apomicts are all capable of some sexual reproduction and, unless the parent is homozygous and self-pollinated, there will be some variant plants among its progeny. The relative proportion of progeny that originate sexually or by apomixis may vary considerably even in the same plant. Therefore, the primary indicator of facultative apomixis is the presence among the progeny of a disproportionately high number of identical offspring that resemble the maternal parent and presumably of hybrid origin. Generally, facultative apomicts do not produce obligate apomictic offspring and those plants that resemble the maternal parent will continue to produce variable progenies. It is known that offspring of some facultative apomicts frequently show a high level (up to 98%) apomictic reproduction.

Detection of apomixis in relatively homozygous or self-pollinated plants by morphological indicators would probably occur only in a plant breeding or genetics program. The most obvious evidence of apomixis would be expected in a hybridization program. Assuming that the breeder's normal emasculation technique is reliable, or that the female parent is male-sterile, the appearance of maternal type plants among or instead of F_1 hybrids would suggest possible apomixis. Other indications of apomixis would be failure of F_1 hybrids to segregate normally, or the sudden appearance of true-breeding lines in early generation progenies.

Other reliable indications of apomixis exist when chromosome number, meiotic behavior, and fertility of a biotype are known. For example, an aneuploid chromosome number that is constant for the biotype or good seed production in plants with great meiotic irregularity provide good evidence of apomixis (Muntzing, 1933). Fertility in triploids, hybrids from wide crosses, and other plants normally expected to exhibit sterility, also suggest apomixis. A high percentage of twin seedlings is frequently encountered in aposporous apomicts. I have observed identical twins (up to 22%) and occasional triplets in buffelgrass as a result of apospory. Facultative aposporous apomicts often produce one embryo in the sexual embryo sac and one or more embryos in apomictic sacs. Uniformity in protogynous species, where early stigma exsertion may enforce crossing, might also indicate apomixis.

The breeder should be alert for any unusual breeding behavior that might suggest deviation from sexual reproduction. Spontaneous increase in the ploidy level of an offspring may suggest unreduced gametes and a tendency toward apomixis. At best, these are only indicators of apomixis that may serve to encourage further studies to confirm the method of reproduction.

IV. TECHNIQUES FOR CONFIRMING APOMIXIS

A progeny test combined with cytological study of megasporogenesis and embryo sac development are usually required to confirm the presence of apomixis and to identify the mechanism. Neither study alone is adequate for conclusive results. As noted previously, the mechanism of apomixis is determined by observing the source and subsequent development of the cell that gives rise to the apomictic embryo. This can only be determined by cytological studies. Unfortunately, cytological observation does not indicate how frequently an asexual seed is formed in facultative apomicts. This information is gained by observing the percentage of maternal-like plants among the progeny. Often the potential for apomictic reproduction is far greater than the percentage of apomictic embryos developed. Some strains of Kentucky bluegrass regularly produce aposporous embryo sacs in over 98% of the ovules, but the percentage of their offspring produced by apomixis may be far less. With highly heterozygous plants, the progeny test provides a reliable estimate of the frequency of apomixis, but it tells nothing about the mechanism involved except for parthenogenesis. Results of studies of selfed progeny of relatively homozygous plants are usually inconclusive. Here one must attempt to cross the suspected apomictic plant with a male parent carrying a dominant marker.

Cytological study of method of reproduction is critical and deserves special consideration. In apospory, replacement of the functional megaspore by an aposporous cell may occur quickly and unobserved. This is particularly critical in species in which the aposporous sac differentiates fully and closely resembles a sexual embryo sac. Where differentiation is limited or numerous aposporous sacs are formed, identification is relatively easy. Identification of diplospory is even more difficult because of the small size and early age of the ovule when meiosis occurs. To detect diplospory, one must determine whether first division of a megaspore mother cell is meiotic or mitotic. The meiotic stage can easily be missed in ovules collected for study because three members of the linear tetrad of megaspores nearest the micropyle usually abort and disappear early in a sexual plant. To identify both apospory and diplospory, one must observe individual ovules representing all stages of development from initiation of the megaspore mother cell to formation of the mature embryo sac.

The Paraffin sectioning is a reliable method for systematically examining anatomical features in the ovule because it preserves spatial relationships essential for correct interpretation. For accurate determination of mechanism of apomixis, it is necessary that the ovule be aligned to give true longitudinal sections through gametophytic tissue. Events that occur during megasporogenesis, especially presence or absence of a linear tetrad of mega-

spores, abortion during or following meiosis, and the appearance of adjacent nucellar cells are critical factors in the identification of the apomictic mechanism. The safranin-fast green stain (Johansen, 1940) is usually satisfactory for overall morphological features and resting nuclei. A good chromatic stain, such as hematoxylin, is essential if chromosome details are desired.

Embryo sac squash techniques (Bradley, 1948) are often useful for study of mature ovules, especially if one desires to see the intact contents of the embryo sac. I have encountered problems with this technique in certain apomictic species that have multiple embryo sacs. It is extremely difficult to distinguish between nucellar embryo sacs and antipodal cells in species in which the antipodals divide profusely. The paraffin section technique is definitely preferred over ovule squashes for study of early megasporogenesis.

Several excellent clearing techniques are available for observation of internal details of ovaries using the phase contrast microscope. These preparations permit viewing the ovule as a unit and show all cellular detail in proper context. A methyl salicylate technique suggested by Crane (1978) has given good results with small ovaries of grass. It is helpful for the cytologist to first become familiar with typical apomictic mechanisms using the paraffin section technique before using squashes or clearing methods.

V. GENETICS OF APOMIXIS

Apomictic species have been poor subjects for genetic study in the past. The data for most experiments have not been conclusive enough to establish the exact mode of inheritance or to permit identification of specific genotypes that condition apomixis. Results of the successful crosses between sexual and apomictic plants that have been reported indicate that the basic processes responsible for apomictic reproduction are genetically controlled. Most of the earlier research was conducted with facultative apomicts, which are capable of both apomictic and sexual reproduction at the same time. Inheritance data from facultative apomicts generally have been confusing and difficult to interpret because there is no certain way to determine whether individual offspring originated from sexual or apomictic reproduction.

Fairly recent discovery of completely sexual plants in species that are predominantly obligate apomicts opened up new opportunities for genetic studies. These plants are capable of only one method of reproduction, apomixis or sexual, and the origin of each offspring is known. Hybrids and progenies from crosses of purely sexual plants with obligate apomicts provide data that can be accurately analyzed statistically for fit to hypothetical ratios. There are a few reports available from these crosses that present reliable inheritance data.

Results of studies conducted with buffelgrass, an aposporous apomict, showed that method of reproduction is controlled by two genes and epistasis (Taliaferro and Bashaw, 1966). These experiments were conducted with selfed progenies of a rare sexual plant that is heterozygous for method of reproduction, and with hybrids produced by emasculating the sexual plant and pollinating it with pollen from obligate apomictic plants. Data on

method of reproduction of 614 selfed progeny gave a sexual to apomictic ratio of 13:3. When the sexual plant was crossed with two different obligate apomictic biotypes the frequency of sexual to apomictic F_1 hybrids fit a 5:3 ratio. On the basis of these data, the genotype of the sexual parent was hypothesized to be *AaBb*, where dominant gene *A*, under conditions sexual reproduction and is epistatic to dominant gene *B* conditions apospory. Under this hypothesis, the genotype of the two apomictic male parents would be *Aabb*. Assuming that the double recessive *aabb* would reproduce sexually because of the absence of the dominant *A* gene, one would expect the 13:3 and 5:3 ratios observed in the experiments.

When the sexual buffelgrass plant was crossed with birdwoodgrass, a closely related apomictic (obligate apospory) species, the same ratios were obtained in the F_1 generation (Read and Bashaw, 1969). Subsequently, the sexual plant was crossed with a plant having the only other possible genotype for apomixis, *AAbb*. This is comparable to a test cross for mode of reproduction, and the resultant hybrids comprised the expected 1:1 ratio of sexual to apomictic plants. These results confirmed the hypothesized genetic model and showed that obligate apospory can be manipulated just as other genetic characters in a breeding program.

Somewhat similar results were obtained from an experiment with bahiagrass (Burton and Forbes, 1960). The common tetraploid biotype of this species is an obligate aposporous apomict, but a diploid strain ('Pensacola') is completely sexual. The chromosome number of the diploid was doubled and the resultant sexual autotetraploid was successfully crossed with the common apomictic biotype. F_1 ratios obtained from this cross suggested that apomixis was recessive to sexuality and controlled by a few recessive genes. The data were close enough to expected autotetraploid ratios to permit postulation of an *aaaa* genotype for the apomictic parent.

Little is known about the inheritance of diplospory. Here the mechanism for development of the apomictic embryo sac differs entirely from apospory. Meiosis is somehow suppressed and the unreduced megaspore mother cell is stimulated to form a functional embryo sac by mitotic division. The few experiments that have been conducted with diplosporous apomicts indicate that this mechanism is also genetically controlled. Both sexual and diplosporous and apomictic plants were recovered among the progeny of a cross of sexual and apomictic weeping lovegrass (Brix, 1974; Voigt and Bashaw, 1972, 1976). There is not enough information at this time to explain the genetics of diplospory, but the data suggest simple inheritance.

Transmission of apomixis to hybrid progenies has been demonstrated in some cross-pollinated facultative apomicts by using genetic markers to identify the offspring of sexual origin. Experiments in numerous unrelated genera clearly indicate a genetic basis for apospory in facultative apomicts, but mode of inheritance seems to vary in different species. In guayule, conditions necessary for expression of apomixis appeared to be conditioned by three recessive genes (Powers, 1945). Results of studies with the *Bothriochloa-Dichanthium* complex indicated that apomixis was dominant to, but independent of, sexuality and controlled by no more than one gene per genome (Harlan et al., 1964). Apomictic tetraploid plants were assigned the genotype *Aaaa*, and the sexual ones the genotype *aaaa*. Experiments with guineagrass also indicated that sexuality in that species is dominant to

apomixis and that method of reproduction is probably controlled by two loci (Smith, 1972; Hanna et al., 1973).

There is yet no biochemical or physiological information on the factors responsible for apospory. This information is needed as a basis for understanding the nature of gene action in apomixis and the fundamental difference between mechanisms. A comparison of the genetic data from aposporous apomicts with observed cytological behavior suggests that one genetic factor serves to activate nucellar cells, causing otherwise senescent tissue to become meristematic and produce unreduced aposporous embryo sacs while simultaneously suppressing development of the sexual tissue. Apparently a second factor, when dominant, completely nullifies the activating factor and restores sexuality. It would seem that a primary difference between obligate and facultative aposporous apomicts is lack of suppression of sexual development in the facultative type.

VI. HYBRIDIZATION AND BREEDING OF APOMICTS

Apomixis can either prevent breeding progress or be a useful tool of the plant breeder. The first requirement for successful improvement of apomictic species is the availability of sexual or partially sexual plants for use as female parents in a hybridization program. Except for occasional fertilization of an unreduced egg, an obligate apomictic plant cannot be used as the female parent. Most apomicts produce viable pollen and can serve as male parents just as sexual plants. Once sexual or partially sexual plants are discovered, the success and efficiency of the breeding program depends largely on whether the species is an obligate or facultative apomict. Apomictic plants generally are highly heterozygous and when the apomictic barrier is broken, there is abundant variability from which to select new types. Apomicts do not usually require special crossing techniques. Hybridization methods described in later chapters for sexual plants should be effective for sexual × apomictic crosses in those crops. Since apomictic plants tend to be highly heterozygous and hybrids may be difficult to identify, reliable methods of emasculation and genetic markers are important in plants subject to self pollination.

A. Obligate Apomicts

Obligate apomixis can be used as an effective plant breeding tool once sexual plants have been identified in the species. The principle involves control and manipulation of method of reproduction through hybridization with obligate apomicts in the species. Depending upon the inheritance of apomixis, a portion of the offspring in the F_1 and succeeding generations will reproduce by obligate apomixis and breed true. Heterosis, when present in apomictic progeny, will be permanently fixed in succeeding generations. For maximum efficiency, the breeder must determine the genetic constitution of the parents and obtain inheritance data on important characteristics as in any improvement program. When this information is available and the appropriate apomictic male parents are selected and crossed with the sexual
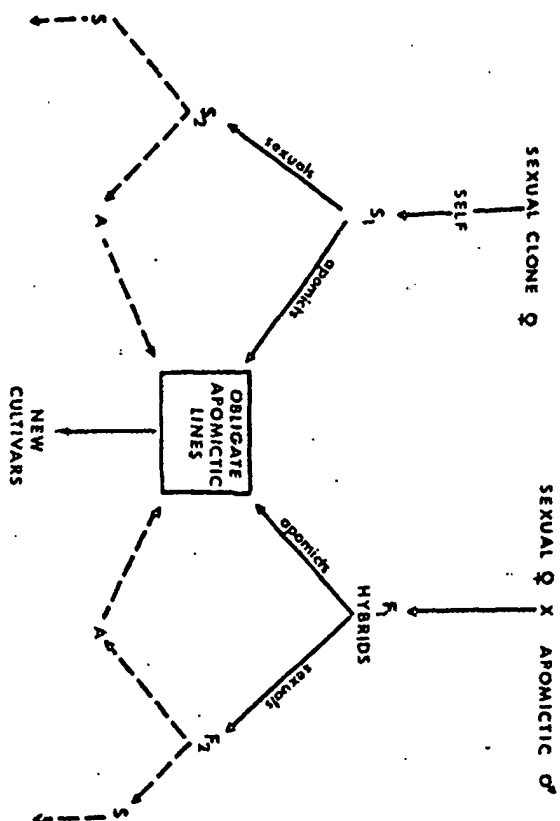
plant, one simply selects and tests the apomictic offspring that appear to have the desired combination of agronomic traits. Apomictic plants also may be selected in succeeding generations because some sexual progeny will continue to segregate for mode of reproduction.

The procedure used in the breeding of apomictic buffelgrass and bird-woodgrass is illustrated in Fig. 3. With these species, we use a heterozygous, sexual, buffelgrass plant as the female parent and cross it to various apomictic male parents. The resultant apomictic F_1 hybrids are obligate apomicts and breed true while sexual hybrids from the same cross produce segregating progenies (Fig. 4). The sexual plant is heterozygous for method of reproduction, therefore its selfed progeny also provide a source of apomictic plants for selection. The first apomictic cultivar, 'Higgins', released from a buffelgrass breeding program, was selected from selfed progeny of a sexual plant. Primary emphasis in the program is placed on the selection of superior apomictic F_1 hybrids to take advantage of maximum hybrid vigor. Two cultivars, 'Neuces' and 'Llano', were developed in this manner. Selection of apomictic progeny is possible in succeeding generations following hybridization, but there is a risk of some reduction in hybrid vigor. We have noted considerable loss in vigor in F_3 and F_4 progenies of sexual hybrids. A similar situation was observed in bahiagrass in which high forage yield was maintained in apomictic hybrids, but was rapidly lost in generations of the sexual progenies (Burton and Forbes, 1960).

There is no reason to expect that all sexual plants discovered in obligate apomictic species will be heterozygous for method of reproduction. In many cases, one or two generations following hybridization may be required for the expression of apomixis. Early identification of sexual parents with good combining ability and heterozygous for method of reproduction would be desirable. As with any breeding program, not all sexual plants will necessarily be desirable parents. Cytological studies are particularly useful for early determination of mode of reproduction in hybrids because it eliminates the need for conventional progeny tests. Backcrossing sexual F_1 hybrids to their apomictic parents may speed up development of apomictic lines.

If sexual plants are not available in the species, other approaches should be considered. It may be possible to break apomixis through hybridization with sexual plants of closely related species. If the species relationship is close enough, it should be possible to introduce sexuality into the species through interspecific hybridization. Because apomixis tends to preserve fertility by eliminating the sexual mechanism, one may be able to produce useful obligate apomictic, interspecific hybrids with good seed set. A word of caution is in order here because sexual apomixis does not always insure fertility. In pseudogamous species, viable pollen is necessary for seed set, and apomixis would not necessarily overcome sterility in incompatible plants. Apomictic common dallisgrass seldom produces over 40% seed set in spite of an apparently adequate quantity of viable pollen. In this species, the problem seems to be associated with competition for nutrition among the vast number of nucellar embryo sacs formed in the ovule (Bashaw and Holt, 1958). Pollen quality of fountaingrass is extremely poor and few seed are formed from self-pollination. However, when this species is pollinated with buffelgrass pollen, over 20% seed is formed pseudogamously (Simp-

Fig. 3—Diagram of methods used to produce apomictic buffelgrass cultivars. Sexual parent is heterozygous for method of reproduction (Taliaferro and Bashaw, 1966).

Fig. 4—Heterogenous progenies from one sexual (S) F_1 plant and uniform progenies from two obligate apomictic (A) F_1 plants of buffelgrass.

son and Bashaw, 1969). The breeder also should be alert to the possibility afforded by fertilization of an unreduced egg in the apomict. Although this phenomenon is relatively rare, it provides yet another way to introduce new characters. In obligate apomicts, these offspring breed true and may prove immediately useful in the breeding program.

B. Facultative Apomicts

Breeding of facultative apomicts is much more difficult than breeding obligate types because of inability to control variation in their progenies. The presence of some sexuality in each plant allows for hybridization, but the progenies continue to segregate for method of reproduction through succeeding generations. In spite of this fact, some useful cultivars have been developed, especially in forage crops in which some degree of variability may not be a serious problem (Kentucky bluegrass, guineagrass, bluestem).

There are several important factors to consider in planning a breeding program with facultative apomicts. The fact that highly apomictic offspring are often produced by these species provides an opportunity to reduce variation. It would be advantageous to select highly apomictic parents for hybridization because these progeny tend to retain a high level of apomixis. Choice of parents that are relatively similar in important characteristics, such as height and maturity, also should be considered. As I mentioned earlier, the use of parents with distinctive marker characteristics will greatly facilitate identification of hybrids and detection of variation in succeeding generations. Perhaps the most important factor in breeding of facultative apomicts is to determine the stability of each line through several generations before releasing a cultivar. Problems in commercial seed production are discussed in Section VIII.

C. Possibilities for Inducing Apomixis

Breeders of sexual species may wish to find sources of apomixis because of its potential. This raises the question of possibilities for inducing apomixis into sexual species. Apparently no research has been designed specifically to induce apomixis, but results of other studies suggest several possibilities, including mutation. One of the first apomictic strains of grain sorghum was derived from irradiated stock (Hanna et al., 1970). Facultative apomixis was observed in pearl millet following treatment of seed with thermal neutrons and diethyl sulfate (Hanna and Powell, 1973). I believe that the sexual buffelgrass plant described earlier originated as a spontaneous mutation from apomixis to sexuality. These results suggest that induction of apomixis by mutation is feasible, but there are no general rules for identifying candidate species for this research. Perhaps the best possibilities would be species with known apomictic wild relatives. Transfer of apomixis from these relatives through hybridization would seem to offer a more promising approach at this time. At present, we lack the necessary information on the physiological basis of apomixis to plan experiments involving

growth regulators. When the basic factors responsible for initiation of apomictic embryo sacs are understood, chemical induction of apomixis or sexuality may be possible.

VII. ENVIRONMENTAL EFFECTS ON APOMIXIS

Environmental factors may affect the stability of the reproductive process in facultative apomicts, but such effects have not been observed in obligate apomicts. Apomictic and sexual embryo sacs develop simultaneously in aposporous facultative apomicts, such as Kentucky bluegrass, and apparently there exists a delicate balance in the competition for survival within the ovule. Sometimes environment can upset their balance in favor of one of these gametophytes. For example, cytological studies of several strains of Kentucky bluegrass showed that aposporous embryo sacs developed in at least 98% of the ovules of each strain. However, when these strains were grown under diverse environments, a higher frequency of aberrant and weak plants occurred among the progeny when seed was produced over a wide range of anthesis and short photoperiod as compared with a narrow range of anthesis and long photoperiod (Hovin et al., 1976).

Day length had a significant effect on the relative frequency of apomictic and sexual embryo sacs in ovules of Dichanthium aristatum (Poir.) C. E. Hubb. Over 14 hours of daylight during development of inflorescences resulted in a much lower incidence of apomictic sacs than day lengths less than 14 hours (Knox and Heslop-Harrison, 1963; Knox, 1967). Results of cytological and breeding studies with Kentucky bluegrass revealed 15 different ways in which embryos may develop (Grazi et al., 1961). These results show the importance of knowing the potential sources of variation, as well as the characteristic behavior of specific germplasm in succeeding generations and under diverse environments.

Thus far, we have not observed environmental effects on embryo sac development in obligate apomicts or the possible appearance of facultative apomixis in succeeding generations from obligate apomicts. After hybridization of sexual plants with obligate apomicts, it was found that the F1 offspring and their progenies have always been either completely sexual or obligate apomicts. Environment sometimes does affect pollen quality, an important factor in pseudogamous apomicts. Environment may also affect the total number of aposporous embryo sacs that develop in an ovule.

The possible effects of environment on diplospory are not known. Such effects could be important in these species because only one embryo sac, either sexual or apomictic, is formed and the potential for embryonic development is far less than in most aposporous apomicts.

VIII. SEED PRODUCTION OF APOMICTS

Commercial seed production of obligate apomicts is simple and involves the same general principles that apply to vegetatively reproduced cultivars. There is no danger of outcrossing in these species, and isolation is

required only to prevent mechanical mixture during harvest. With buffelgrass, we normally skip two rows between seed production plots. All classes of seed are genetically the same because there are no sexual generations from an obligate apomict. A seed field of perennials can be maintained indefinitely, if it is kept free of contamination by other species and volunteer plants of other strains of the same species. The use of male sterility to facilitate hybridization of sexual plants with pseudogamous apomicts would require that fertility be restored in the F_1 because pollination is required for seed development.

Seed production of facultative apomicts requires special considerations, especially regarding establishment of standards. First, the breeder must determine the degree of variation that is acceptable for a particular crop. One must then determine the nature and extent of variation characteristic of each line. This information can only be determined by growing the line for sufficient generations to obtain a history of variability. Because environment may affect mode of reproduction, all advanced strains should be evaluated for variation in the area and under those conditions expected where commercial seed production is anticipated. Usually all plants in facultative apomictic lines will be capable of some sexual reproduction, and the proportion of sexual to apomictic progeny may remain relatively stable or increase. Isolation to prevent outcrossing of facultative apomicts is just as essential as it is with sexual species. It will be necessary to establish standards for commercial seed production of each individual line being considered for release. Close cooperation between the breeder, seed grower, and farmer will be required to determine whether a line meets the requirements for purity and uniformity necessary for successful farm production.

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